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NEW LATE MIOCENE FOSSIL PECCARIES FROM CALIFORNIA AND NEBRASKA

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ABSTRACT

We describe two new genera and species of peccaries from the late Miocene of the western United States. Both of these new taxa are referable to the *Macrogenis-Tayassu* clade, but form their own clade united by the presence of a zygomatic wing whose anterior edge protrudes laterally at right angles to the snout. Numerous nearly complete skulls and jaws from Blackhawk Ranch (Green Valley Formation, latest Clarendonian, about 9.0–9.5 Ma) pertain to a new genus and species, *Woodburnehyus grenaderae*. *W. grenaderae* is distinguished from similar taxa by its wide dentary and broad, bulbous cheek teeth. In addition, it is distinct from other species in lacking a contact between the maxillary and the suborbital bulla. Its suborbital bulla is narrows anteriorly, and it has a narrow tympanic process. A second new genus and species, *Skinmerhyus shermorum*, is based on material from the late Clarendonian Merritt Dam Member, Ash Hollow Formation, north-central Nebraska. It has remarkable laterally flaring wing-like zygomatic processes, and it is distinguished from other members of the *Macrogenis-Tayassu* clade by having an anterior atrial aperture medial to M1, and the anterior palatine foramen medial to M1. The high diversity of peccaries at this time is largely a function of their disparate array of zygomatic crests in male skulls.

Introduction

The peccaries or javelinas (family Tayassuidae) are a group of suiform artiodactyls with a long history in the New World. Although they look somewhat similar to pigs, the tayassuids are a separate family that split off from true pigs (family Suidae) more than 37 million years ago. Since then, they underwent a long evolutionary history in North America before spreading to South America in the late Miocene. Today peccaries are found largely in Central and South America, although they also occur in the southwestern deserts of the United States. Three species still survive: *Dicotyles tajacu*, the collared peccary; *Tayassu pecari*, the white-lipped peccary; and *Catagonus wagneri*, the Chacoan peccary. This last species was known only from fossils until living populations were discovered in the Gran Chaco of Paraguay in 1975. However, peccaries were much more diverse over the past 37 million years, with at least 20 genera and an unknown number of valid species represented in the fossil record of North America.

Despite their abundant fossil record in North America, and large new collections with excellent skulls in many museums (especially the Frick Collection in the American Museum of Natural History in New York), there has not been a significant published description of most of these fossils yet. Prothero (2009)

published a revision of the early radiation of North American Eocene-Oligocene peccaries, but that study did not deal with the Miocene forms. In 1983, David B. Wright did his master's thesis at the University of Nebraska on some late Miocene peccaries, and in 1991 he completed a doctoral dissertation on Neogene peccaries at the University of Massachusetts. Except for a few short peripheral papers (e.g., Wright, 1993), and a short summary chapter that provided no detailed descriptions or new names (Wright, 1998), none of Wright's work has been published, and it has been more than 20 years since he left the profession. Because no one else has taken up the task of finishing Wright's work and properly naming and describing these new fossils, we have begun to do so in this paper. Most of Wright's descriptions were sound, but they are not widely available to the scientific community since they remain in unpublished theses. Thus, we have re-described the fossils as much as possible, or when necessary, paraphrase from Wright's unpublished theses, since we are in agreement with most of his conclusions.

Materials and Methods

This study began as a student research project by Pollen and was presented at the 2011 Society of Vertebrate Paleontology

meeting in Las Vegas (Prothero and Pollen, 2011). It is published separately here, but it is part of a much larger complete monographic revision of the Tayassuidae currently being written (Prothero in prep.). Specimens were measured with digital calipers and data entered and statistically analyzed using Excel spreadsheets. The photos were taken with a Nikon 5700 camera, and edited in Photoshop.

Museum Abbreviations: AMNH, American Museum of Natural History, New York, New York, including the Frick Collection (F:AM); UCMP, University of California Museum of Paleontology, Berkeley, California.

Systematic Paleontology

Class MAMMALIA Linnaeus 1858
 Order ARTIODACTYLA Owen 1848
 Family TAYASSUIDAE Palmer 1897
Woodburnehyus n. gen.
 Figures 1–4, Tables 1–2

Type and only species

W. grenaderae.

Diagnosis

Same as for *W. grenaderae*.

Etymology

In honor of Dr. Michael O. Woodburne, for his many contributions to the understanding of fossil peccaries and Miocene localities such as Blackhawk Ranch, plus *-hyus*, Greek for “pig”.

Type and only locality

Blackhawk Ranch Quarry, UCMP locality V3310, Green Valley Formation, Contra Costa County, California; late Clarendonian in age (see Prothero and Tedford, 2001).

Description

Same as for *W. grenaderae*.

Discussion

Wright (1983, 1991, 1998) recognized the distinctiveness of the Blackhawk Ranch peccary specimens, but never published a description of that material, nor did he give it a taxonomic name even though he recognized that it was clearly a new genus and species. In those publications (especially his 1998 summary chapter) it was just referred to as the “Blackhawk Ranch species”, but no adequate justification was given for his taxonomic decisions. Wright (1983) refers to this species as “Species F” in his unpublished master’s thesis. In the UCMP data base, the published literature, and in online faunal lists of the locality, this material is incorrectly referred to *Prosthennops*, which is a wastebasket taxon for late Miocene peccary taxa with teeth which are low-crowned and bunodont (Wright, 1998; Prothero in prep.).

Woodburnehyus grenaderae n. sp.

Diagnosis

A peccary from the *Macrogenis-Tayassu* clade distinguished from all other members of that clade (including *Skinnerhyus*) by its relatively broad and robust dentary and wide, bulbous cheek teeth. It also lacks a contact between the maxillary and the

suborbital bulla, and the auditory bulla and tympanic process are relatively narrow. The facial crest or zygomatic wing is quite short and blunt, with the anterior edge protruding laterally and perpendicularly from the facial region, and extending anteriorly over the rostral muscle fossa. These features distinguish it from *Skinnerhyus*, *Macrogenis*, and other peccaries.

Etymology

In honor of Jessica Grenader, for her contributions to peccary paleontology.

Type specimen

UCMP 74812, partial skull with right and left P2-M3, lacking rostrum anterior to P2 and region posterior to orbit (Figure 1A–C).

Distribution

From type locality only.

Referred material

UCMP 39470 (Figure 2A–B), partial skull with left and right canines, P2-M3; UCMP 77675, partial skull with right P4-M2 (Figure 2C); UCMP 33738, right maxillary fragment with dP4-M1; UCMP 125191, right dp3; UCMP 47325 and 125290, left P3; UCMP 58535, right P3; UCMP125283 and 125287, left P4; UCMP 125293, right P4; UCMP 33739 and 125285, left M2; UCMP 90144, 125281, right M2; UCMP 64413, left M3; UCMP 125286, right M3; UCMP 36471, partial jaw with left p2-4, m2-3, right p3-m2; UCMP 34638, right ramus lacking symphysis or condyle, m1-3 present (Figure 3A–B); UCMP 33737, left ramus with p2-m2 (premolars erupting)(Figure 3C–D); UCMP 34665, left ramus with p3-m3; UCMP 49865, right ramus with p4-m3; UCMP 65217, left ramus fragment with m2; UCMP 34639, left lower canine; UCMP 125288, right dp3; UCMP 125289, right p2; UCMP 90155, right p3; UCMP 125284, right p4; UCMP 90156 and 125282, left m1; UCMP 34672 and 90142, left m3; UCMP 90143 and 125292, right m3. Over 66 specimens of this taxon are listed on the UCMP online catalogue, so there are many additional specimens not included here.

Description

There are four partial skulls that give a reasonable picture of the complete skull anatomy of *W. grenaderae*: UCMP 33736, 39470, 74812, and 77675 (Figures 1–2). The description below is modified from the unpublished work of Wright (1983, pp. 174–175), and represents a composite description based on these four skulls and additional material in the Blackhawk Ranch collection.

In lateral view (Figure 1C, 2C), the frontal bones slope anteriorly as in most Clarendonian peccaries. On UCMP 74812 (Figure 1A–C), there are large canine buttresses as well as a large canine, which is presumed to represent a male individual. However, UCMP 39470 (Figure 2A–B) has much smaller canines and buttresses, so it probably represents a female specimen. Similar sexually dimorphic canines and canine buttresses are widely observed in the peccaries (Wright, 1983), and can be seen in living peccary populations. *W. grenaderae* has relatively short premaxillae compared to other species from the Clarendonian. There is a strong buccinator ridge on the snout, particularly well shown on UCMP 74812.

The zygomatic wings or facial crests of *W. grenaderae* are distinct from those of any other peccary known, and distinctive enough from *Macrogenis*, *Skinnerhyus*, and other genera that a

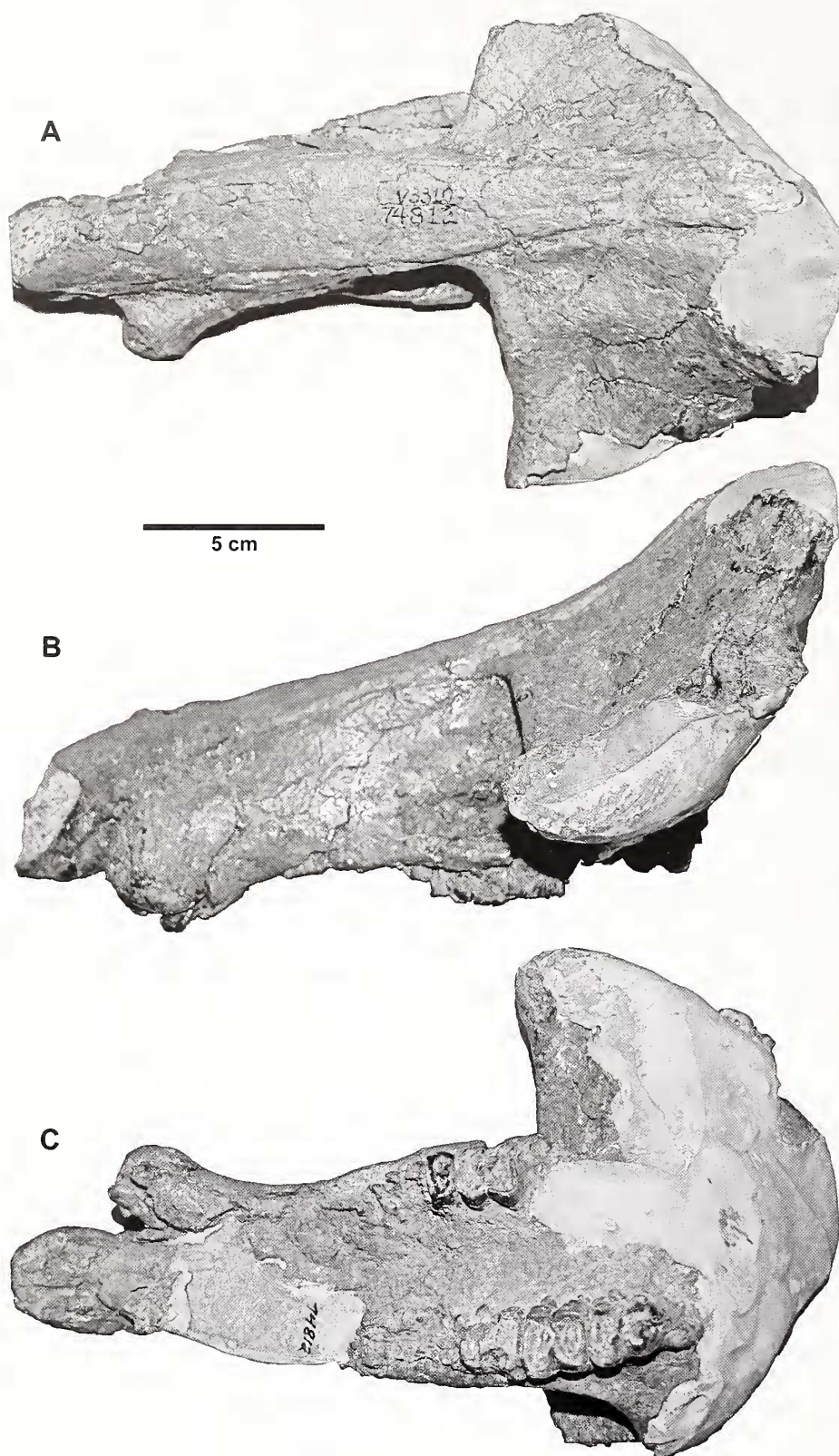


Figure 1. *Woodburnchynus grenaderae*, UCMP 74812, type specimen. A, dorsal, B, left lateral, and C, ventral views. Scale bar equals 5 cm.

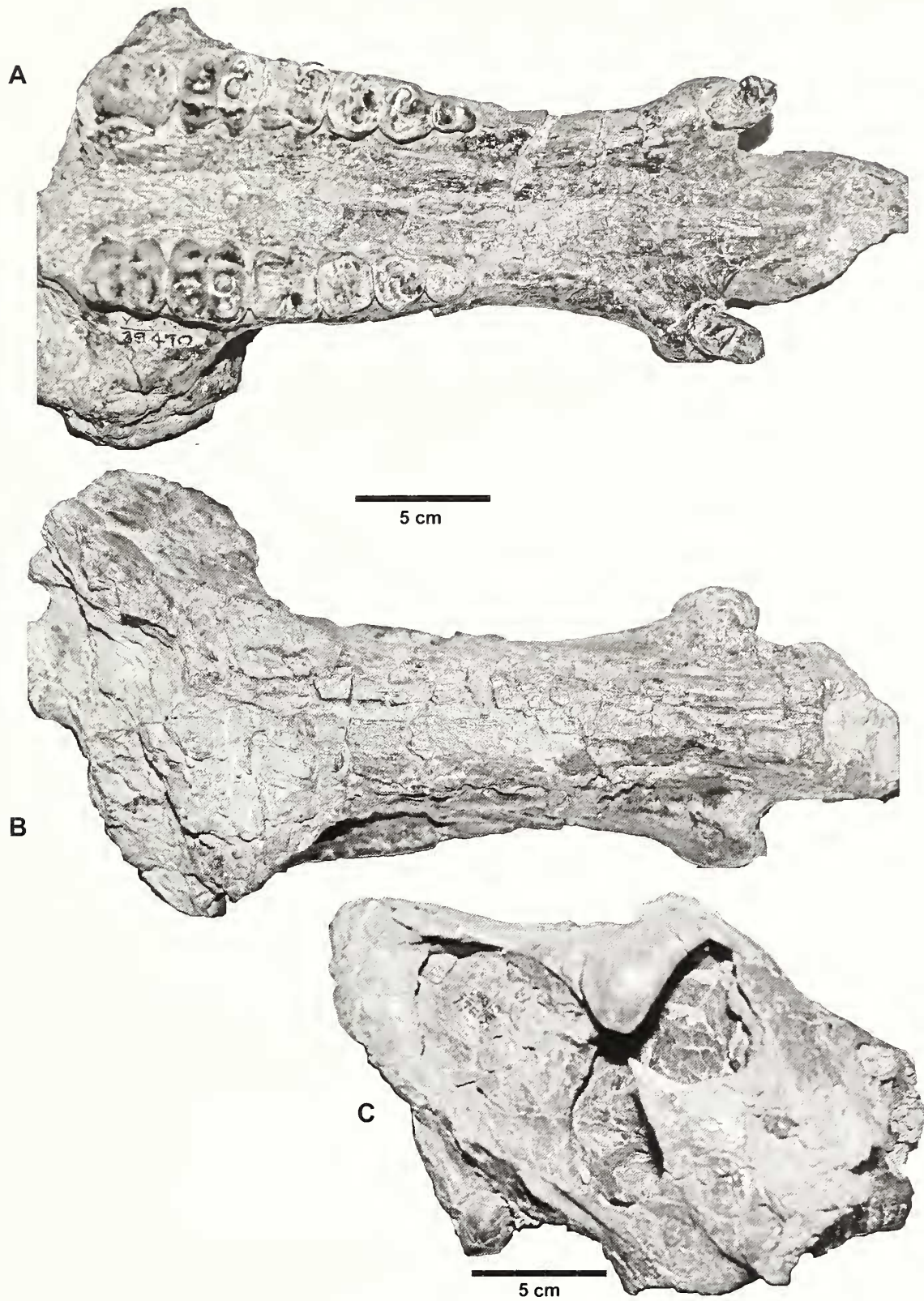


Figure 2. *Woodburnehyus grenaderae*. UCMP 39470, referred female skull. A, ventral, and B, dorsal views. C, UCMP 77675, referred partial skull in right lateral view. Scale bar equals 5 cm.

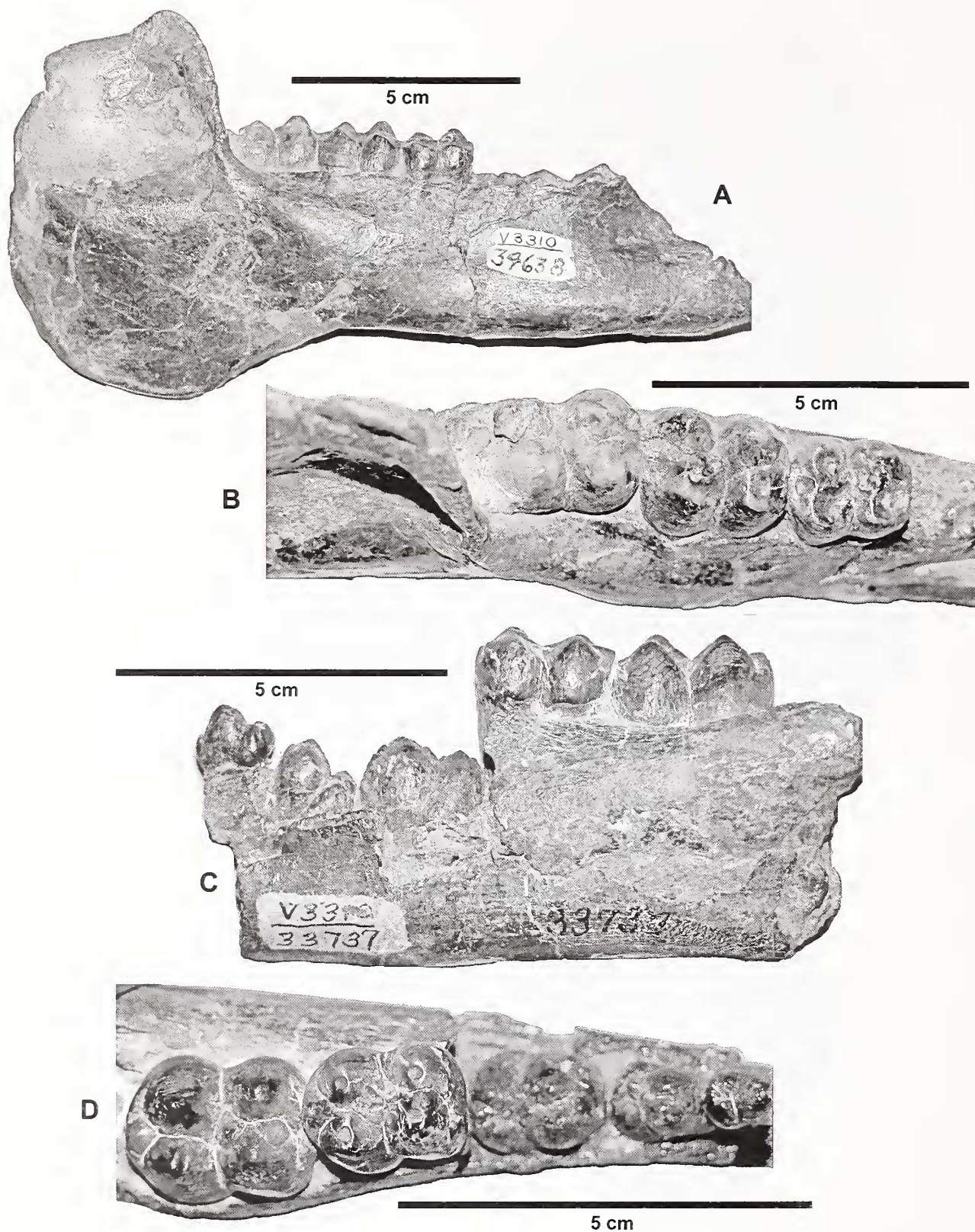


Figure 3. *Woodburnehyus grenaderae*. UCMP 34638, adult ramus. A, right lateral, and B, occlusal views. UCMP 33737, adult ramus with p2-4 still erupting in C, left lateral, and D, occlusal views. Scale bar equals 5 cm.

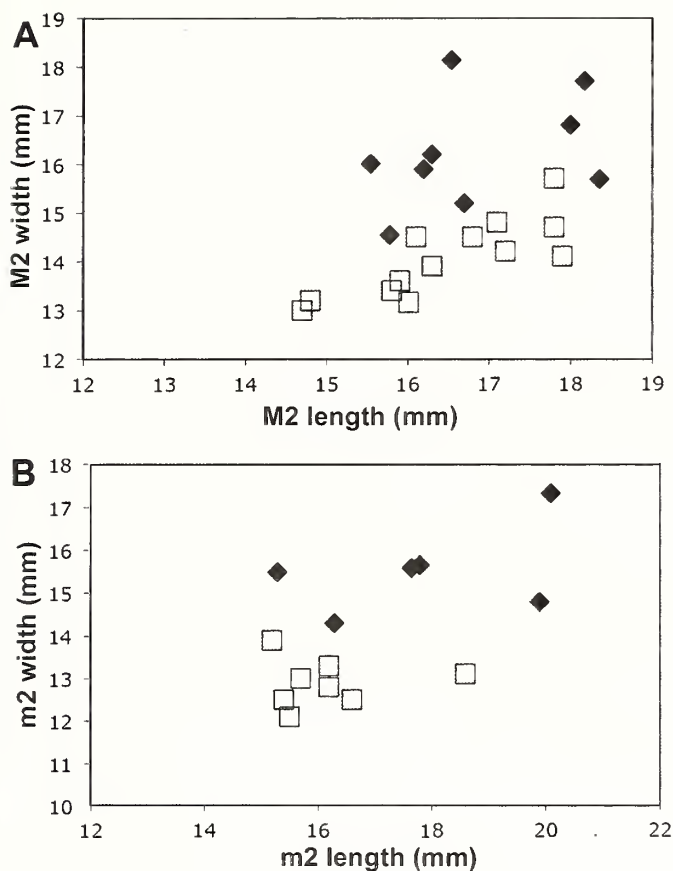


Figure 4. Plot of specimens of *Woodbunehyus grenaderae* versus other peccaries, showing that the lower molars are significantly wider in *W. grenaderae* than in other taxa. A, Comparison of M2 dimensions. B, Comparison of m2 dimensions. Open squares are *S. shermerorum*, solid diamonds are *W. grenaderae*. In every plot, the *W. grenaderae* specimens are broader in tooth dimensions, with no overlap, or only slight overlap with the *S. shermerorum* specimens.

new genus is justified. In nearly all UCMP specimens, the distal portion of the zygoma is broken, but the proximal portion is known from three different skulls. The anterior edge of the zygomatic wing narrows in the spot where it merges with the dorsal surface of the rostrum right above P4 and M1. The large rostral muscle fossa extends beneath the anterior edge of the zygomatic wing, as in *Skimmerhyns shermerorum*. The anterior edge of the zygoma thickens dorsoventrally about 45 mm distal to its origin on the rostrum. Thus, the proximal portion of the zygoma is very similar to the condition seen in *S. shermerorum*.

There is a deep palatine fossa, which is especially well developed on UCMP 77675. The broad pterygoid processes of the alisphenoid flare laterally and meet the palatine bone at an angle of about 130–140°. There is also a large orbitosphenoid bulla, similar in size and proportions to the condition seen in *S. shermerorum*. There is a well-developed glenoid fossa that extends laterally to the edge of the tympanic wing, as seen in *Macrogenis crassigenis* and other Clarendonian peccaries. Most of the specimens lack a well-preserved auditory bulla, but where the bulla is preserved, it seems to have a narrow cross-section, as in many other Miocene peccaries. There is a fragment of juvenile maxilla (UCMP 33738) that preserves the lateral cancellous inflation above dP4 and M1.

The first and second upper incisors are not preserved on any of the skulls known, but their alveoli suggest that the incisors are similar to those of other Clarendonian peccaries. As discussed above and by Wright (1983), the canines show strong sexual dimorphism in both their size and curvature, and also in the size of the canine buttresses from which they protrude.

Most of the dP3 and dP4 specimens in the collection are highly worn, but they are similar to those in other Clarendonian peccaries. All known specimens of *W. grenaderae* have highly worn P2s (Figures 1–2). The P2 has a large protocone, with a smaller metacone posterior to the paracone. The protocone is posterolingual to the paracone. P3 has a trapezoid-like shape in crown view, with the protocone lingual to the paracone as in P2. A crest off the protocone extends anterolabially to join the anterior cingulum. There is a small metaconule, which is surrounded lingually by the hypocone as it fuses with the lingual cingulum. There is a fusion of the two lingual roots on P3. P4 is very similar to the condition in P3, with a large cusp-shaped metaconule fused with the posterior cingulum. Unlike P3, however, the lingual roots appear not to be fused in P4.

The upper molars of *W. grenaderae* are known primarily from very worn teeth, especially M1. In most features, the unworn molars (Figures 1–2) are typical of other Clarendonian peccaries, and their cusp pattern is generalized and non-diagnostic. The most striking feature is that they are relatively wide laterally compared to any other known peccary, and the lower jaw itself is wide and robust compared to those of other peccaries as well (Figure 4). The broad, robust upper and lower cheek teeth and lower jaw is a diagnostic feature for this species.

As was the case for the upper cheek teeth, nearly all the lower cheek teeth are broader and more bulbous than seen in any other peccary (Figure 3). The p2 is like that of most peccaries except that it has a broad, bulbous heel, and a fused protoconid. The robust p3 bears a metaconid with a posterolabial process and a small anterior cusp. The p3 has a distinct, low anteroconid, and its broad heel bears three cusps in unworn specimens (such as the juvenile jaw with the premolars still in their crypts and undergoing eruption, UCMP 33737—Figure 3C–D). The p4 bears a posterolabial process on the metaconid, and most specimens have a cusp on the anterior side of the metaconid as well. The heel of the p4 is very broad, and may bear two large partially fused cusps in unworn specimens, or two large cusps with a smaller cusp in the hypoconulid position, or a large hypoconid and entoconid separated by two smaller cusps. This high variability of cusps in peccaries is why most diagnoses do not rely to heavily on cusp patterns to define species (Colbert, 1938; Simpson, 1949; Wright, 1991, 1998). The molars are much like those of most other Clarendonian peccaries except that they are broader and more bulbous. On the m3, the third lobe bears a single large cusp.

Skimmerhyns n. gen.

Figures 5–7, Tables 1–2

Type and only species

S. shermerorum.

Type locality

Machaerodus Quarry, Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska; late Clarendonian (just beneath an ash dated 9.95 ± 0.8 Ma) (Skinner and Johnson, 1984, p. 315). In some references (e.g., Wright, 1983), the holotype is attributed to “Kat Quarry,” although according to Skinner and Johnson (1984, p. 315), *Machaerodus* Quarry is a separate quarry

Table 1. Comparisons of skull jaw dimensions in the peccary specimens described in this paper. All numbers beginning with 113 are F:AM numbers of specimens of *S. shermerorum*. The other numbers are UCMP catalogue numbers of specimens of *W. grenaderae*. All measurements in mm.

Measurement	113317	113316	113263	39470	74812	77675			
Condylbasal length	324								
Premaxilla length	44.5			37.5	33				
Postcanine diastema	53	58	57	45	39				
Palate posterior to M3	43					30.5			
Canine buttress width	78.9			57.1					
Palate width at M1	26.4			24.1	24.9				
Zygomatic width	295								
Parietal width	125								
Width at glenoid fossa	131.5								
Occiput height	147					135			
Tympanic wing width	126								
Occipital condyle height	24					18.5			
Occipital condyle width	49.1					48			
Foramen magnum height	18.5								
Foramen magnum width	20.6								
Lower jaws	113266	113192	113265	113264	113266	113286	113291	34638	33737
Symphysis length	83.5		81	82.8		87.7	81		
Symphysis width	25.6	21.3	25.6	24		22	27.8		
Diastema length	62.5		64.9	66.1	54.3	62.3	67		
Ramus depth							52.9	31.8	23.5
Ramus width							25.7		23.8

channel within the Xmas Channel-Kat Channel Quarry system, not the same as "Kat Quarry" itself.

Etymology

In memory of Morris Skinner, who discovered the specimen, plus *-hyus*, Greek for "pig".

Diagnosis

Same as for *S. shermerorum*.

Description

Same as for *S. shermerorum*.

Discussion

Wright (1983, 1991, 1998) recognized the distinctiveness of the *Machaerodus* Quarry peccary, but never published a description or a name for this species. In those publications (especially his

1998 summary chapter) Wright referred to as the "*Machaerodus* Quarry species" or "Kat Quarry species", or to his "Species A" (Wright 1983), but no adequate justification was given for his taxonomic decisions. The holotype specimen from *Machaerodus* Quarry (F:AM 113317) and unassociated jaw from Emry Quarry (F:AM 113264) are currently on display in the AMNH fossil mammal hall under the incorrect name *Macrogenis crassigenis*.

Skimmerhyus shermerorum n. sp.

Type specimen

F:AM 113317, male skull (Figure 5).

Referred material

All from quarries in the Merritt Dam Member, Ash Hollow Formation, Cherry County, Nebraska, late Clarendonian (Skinner and Johnson, 1984).

Table 2. Statistics of tooth dimensions in samples of *W. grenaderae* and *S. shermerorum*. N = number of samples; SD = standard deviation.

Dimension	N	<i>W. grenaderae</i>		N	<i>S. shermerorum</i>	
		Mean	SD		Mean	SD
P2L	2	9.4	0.8	3	10.1	0.5
P2W	2	7.8	1.1	3	8.6	0.4
P3L	6	10.8	1.1	6	11.3	0.6
P3W	6	10.7	0.8	6	10.4	1.5
P4L	8	12.3	0.6	8	12.7	0.6
P4W	8	12.6	0.5	8	11.8	1.4
M1L	5	13.9	0.8	9	14.2	0.9
M1W	5	14.5	1.1	9	12.6	0.9
M2L	9	16.8	1.1	13	16.8	0.8
M2W	9	16.2	1.1	13	14.2	0.7
M3L	5	17.8	1.2	5	19.3	0.8
M3W	5	14.5	0.9	5	13.5	1.1
M1-3	4	48	3	1	38.4	—
P2-4	2	31.8	4.4	1	52.4	—
P2-M3	2	79.5	9.5	1	87.3	—

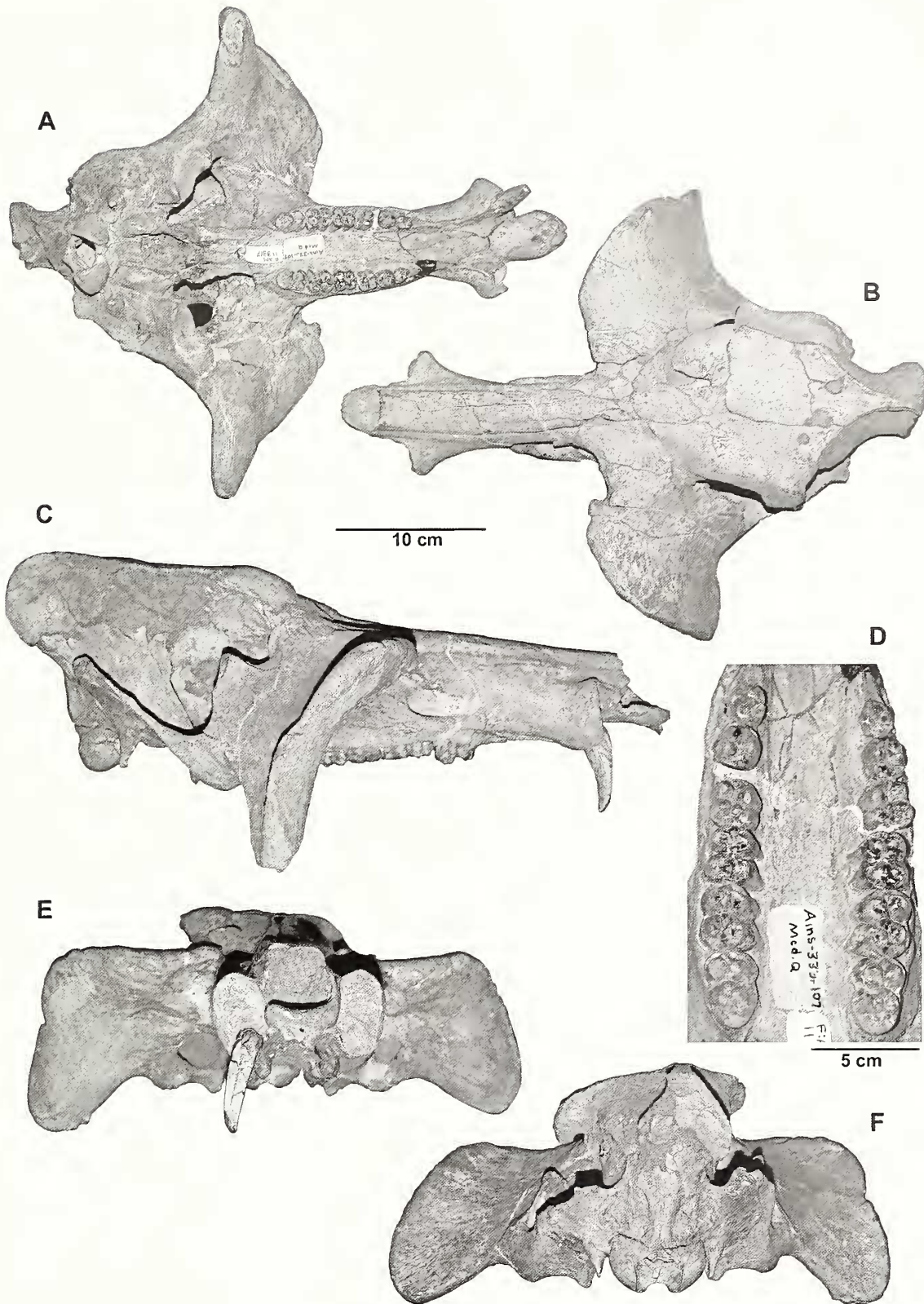


Figure 5. *Skinnerhyus shermerorum*, F:AM 113317, holotype specimen. A, ventral, B, dorsal, and C, right lateral views. D, close-up of upper cheek teeth. E, anterior view showing zygomatic flanges. F, posterior view. Scale bar equals 10 cm.

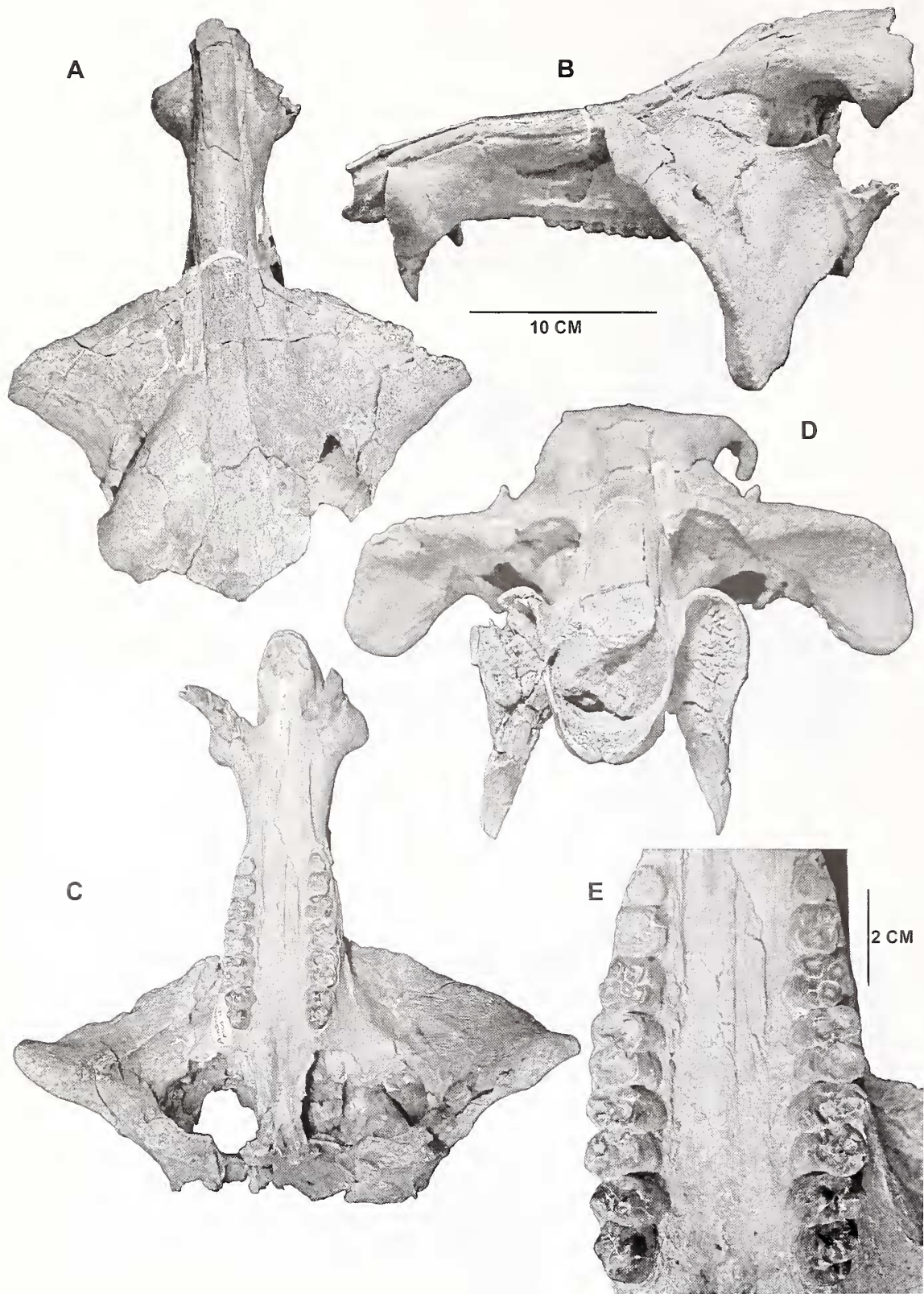


Figure 6. *Skinnerhyus shermerorum*, F:AM 113316, referred specimen. A, dorsal, B, left lateral, C, ventral, and D, anterior views. E, A close-up of upper cheek teeth. Scale bars: (A-D) equals 10 cm; E equals 2 cm. (Photos by Alana Gishlick).

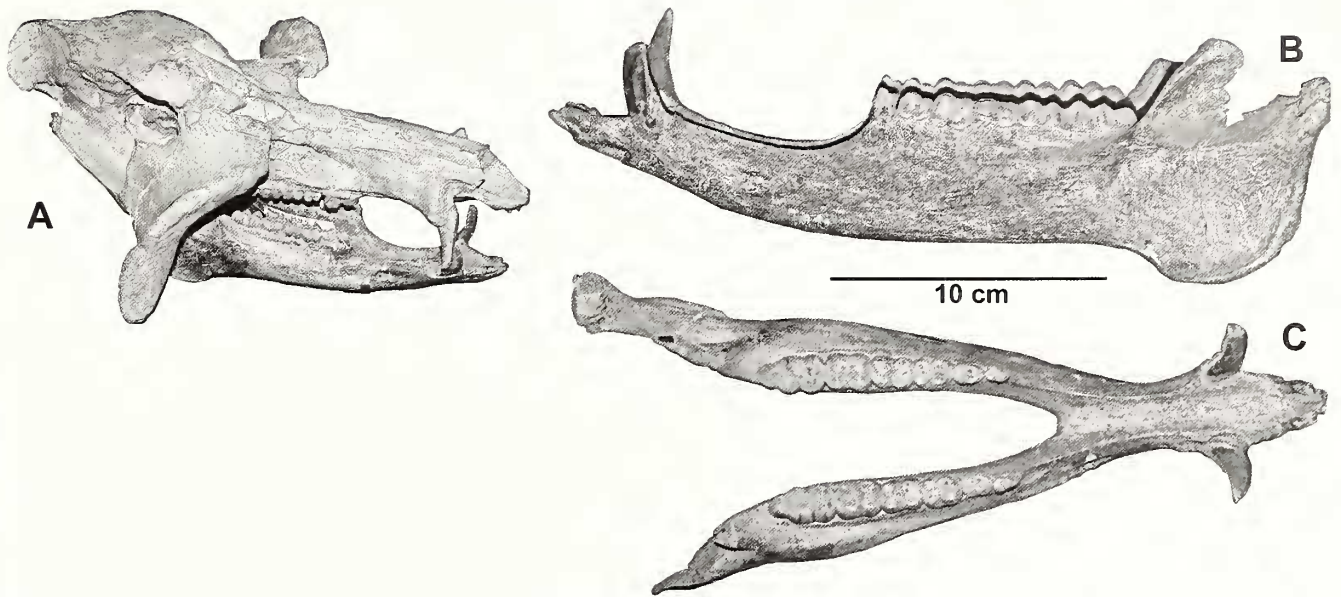


Figure 7. *Skimmerhyus shermerorum*. A, Oblique anterior view of F:AM 113317 (skull) and F:AM 113264 in articulation as they are mounted on display at the AMNH. F:AM 113264, referred lower jaw in B, left lateral, and C, crown views. Scale bar (B and C) equals 10 cm.

From Kat Quarry: F:AM 113316 (Figure 6), partial skull missing basicranial and occipital regions, with left and right canines, P2-M3;

From Emry Quarry: F:AM 113264, lower jaw (Figure 7); F:AM 113259, left maxilla; F:AM 113260, right maxilla; F:AM 113263, partial skull; F:AM 113264, mandible; F:AM 113265, mandible, F:AM 113266, mandible; F:AM 113267, partial symphysis;

From Egger Quarry, F:AM 113193, maxilla; F:AM 113195, maxilla; F:AM 113198, canine; F:AM 113197, dP4; F:AM 113192, partial symphysis; F:AM 113194, left ramus; F:AM 113199, right M2; F:AM 113200, right M1; F:AM 113201, left P4; F:AM 113213, right ramus; F:AM 113214 left ramus; F:AM 113407, right M1; F:AM 143935, left M2;

From Wade Quarry, F:AM 113282, canine; F:AM 113283 canine; F:AM 113284, canine; F:AM 113286, mandible; F:AM 113287, right ramus; F:AM 113288, right ramus; F:AM 113289, right ramus; F:AM 113291, symphysis; F:AM 143934; right P4;

From Xmas Quarry: F:AM 113176, partial palate with left P4-M3; F:AM 113175, partial mandible with left p2-m3, right p3; F:AM 113179, partial left ramus with p4-m3; F:AM 113174, partial right ramus with c1, dp2-4, p4-m2; F:AM 113178, partial right ramus with dp2-4, m1 in crypt.

Etymology—In honor of Dr. Michael Shermer and his daughter Devin Shermer.

Diagnosis

(Modified from Wright, 1983, p. 121): Broad fan-like zygomatic wings that flare outward and upward; deep rostral muscle fossa beneath the anterior edge of the zygomatic wing; glenoid fossa not extending lateral to tympanic wing; no contact between maxilla and lateral edge of orbitosphenoid bulla; narrow auditory bulla; cancellous suprapalatine inflation, with deep dorsal palatine sulcus; moderate-sized premaxilla, about 45 mm in length; nearly spherical occipital condyles compared to other

tayassuines; long upper post-canine diastema (greater than 50 mm); cheek teeth without broad, bulbous shape seen in *Macrogenis*; P2 with protocone, metacone; P3, P4 submolarized.

Description

(Modified from Wright, 183, p. 122–123): *S. shermerorum* differs from *Macrogenis*, *Woodburnehyus*, and virtually all other peccaries in the unique shape of its broadly fan-like zygomatic wings, which extend wider laterally and are more oriented dorsoventrally than in any other tayassuine. On this basis alone, it is clearly a distinct genus, and cannot be referred to any other genus of tayassuid. *S. shermerorum* also has a longer rostrum than that of *Macrogenis*, *Woodburnehyus*, or other peccaries, with large canines and canine buttresses in presumed male skulls (e.g., F:AM 113317, F:AM 113316—Figures 5, 6). The front edge of the zygomatic wing meets the rostrum above M1-2 and ventral to the supraorbital canal. The proximal front edge of the zygomatic wing appears to be straight in dorsal view, and lies perpendicular to the sagittal plane. When viewed from the anterior, the front edge of the zygomatic wing is arched slightly dorsally in F:AM 113317 and markedly so in F:AM 113316, where it forms the dorsal edge of the rostral muscle fossa. On the lateral side of the rostral muscle fossa, the front edge of the zygomatic wing curves posteriorly and ventrally. The distal part of the wing curves in the dorsal direction, especially in F:AM 113317. One feature unique to this species is found in the distal tip of the zygomatic wing, which protrudes ventrally to a position about 3 cm below the glenoid fossa.

When the skull is viewed from the ventral side (Figure 5), the areas of origin for the rostral and masseteric muscles are delimited by sharp crests. The lacrimal foramen is small in F:AM 113317, but in most other specimens it is about the size typical of *Macrogenis* and other late Miocene peccaries. In F:AM 113317, the lateral edges of the palatine bones are parallel, but they converge posteriorly in F:AM 113316. There is a trough-shaped

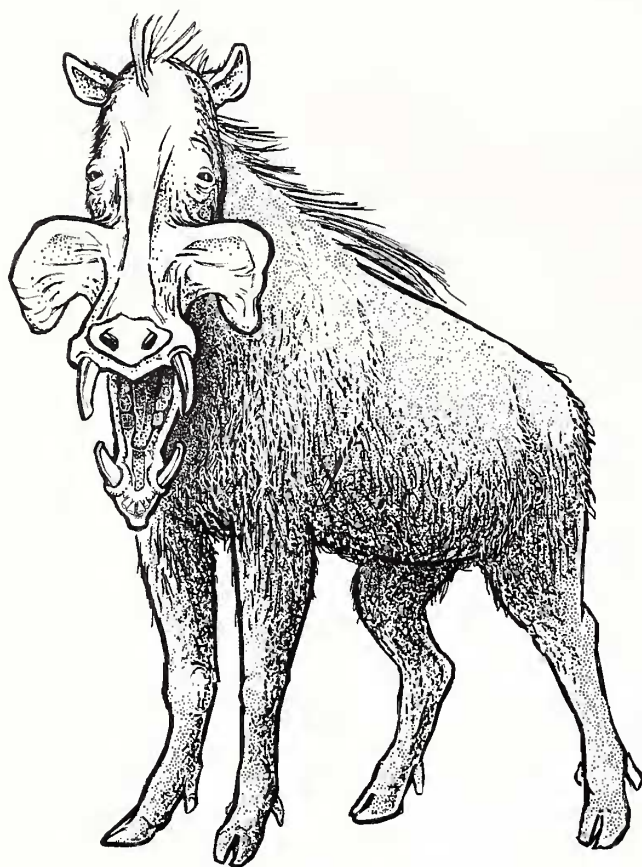


Figure 8. Restoration of *Skinnerhyus shermorum* by Pat Linse.

palatine fossa, which has flat surfaces on each side. The angle between the pterygoid wings of the alisphenoid is about 155° . The pterygoid fossa is elongate, much like that in other late Miocene peccaries. There are no preserved orbitosphenoid bullae in F:AM 113317, but they are large in F:AM 113316, and extend laterally to the level of labial sides of the cheek teeth.

Compared to *M. crassigenis*, the glenoid fossae of *S. shermorum* are not as far laterally from the tympanic wing. There is a concave posterior surface on the squamosal just dorsal to the glenoid fossa. Compared to *Macrogenis* and *Woodburnehyus*, the auditory bullae are not as broad. The occipital condyles are more spherical than is seen in any other tayassuine. The dorsoventral width of the articular surface of the condyle is greater than the lateral width, while the opposite is the case in most other tayassuines.

F:AM 113317 and 113316 have two upper incisors, with I1 being much larger than I2, as in most Miocene tayassuines. The canines show sexual dimorphism in size and shape, as documented by Wright (1993). There is a long canine to P2 diastema. P2 is composed of a distinct protocone and metacone posterior to the paracone, with a thick posterior cingulum. The lingual roots of P3 are fused. P3 also has a small metaconule, and there is a swelling of the posterior cingulum of the hypocone lingual to the metaconule. The paracone, metacone, and protocone of P4 are roughly equal in size. There is a distinct cusp for the hypocone as well, although it is partially joined to the posterior cingulum. The molars of *S. shermorum* show the stereotypical pattern of *Macrogenis*, *Woodburnehyus*, and other late Miocene species.

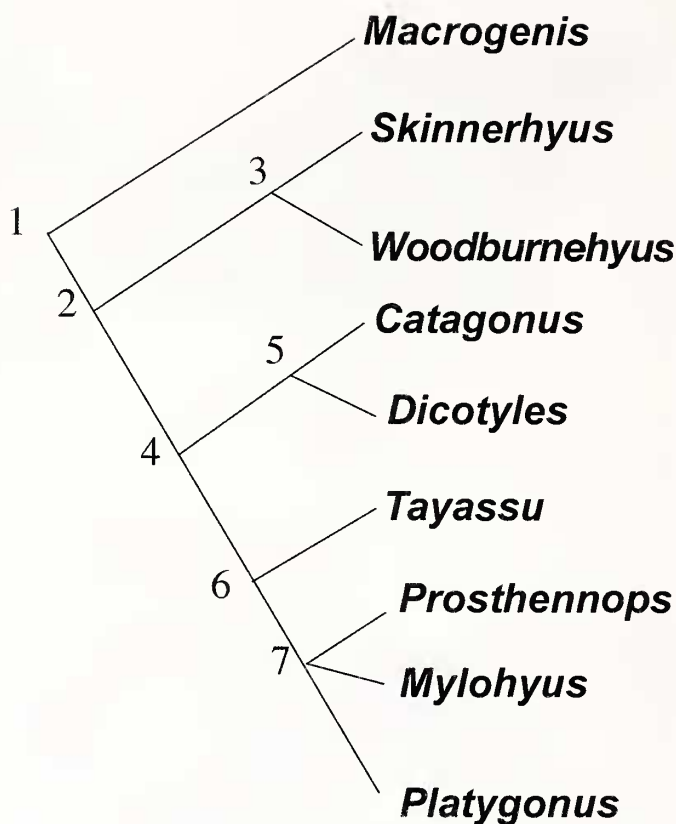


Figure 9. Cladogram of the peccaries discussed in this paper (modified from Wright 1993, 1998). Characters at nodes: 1, *Macrogenis-Tayassu* clade: pneumatic zygomatic arch; anterior palatine foramen lies anterior to M1; I3 absent; p3 lacking paraconid, and with large talonid cusps; 2, facial crest of zygoma extends anteriorly and dorsal to P4; 3, *Woodburnehyus-Skinnerhyus* clade: anterior edge of zygomatic wing is straight and extends perpendicularly from facial region; 4, *Catagonus-Tayassu* clade: tectum of maxillopalatine labyrinth meets nasal septum dorsal to floor of nasal cavity; atrium of maxillopalatine labyrinth subangular in cross-section; P4 with entoconid, hypoconulid; P2 protocone lingual to paracone; p2 with metaconid; dp2 with metaconid; 5, *Catagonus-Dicotyles* clade: pterygoid processes of alisphenoid converge medially at choanal margin; posterior palatine foramen opens within nasal cavity, anterior to sphenopalatine foramen; zygodonty present in some specimens; large suborbital bulla having sharp lateral crest; 6, *Platygonus-Tayassu* clade: deep nasal incision, which is pointed posteriorly; 7, *Prosthenops-Mylohyus-Platygonus* clade: atrium of maxillopalatine labyrinth having posterior aperture; dp2 with protocone.

The lower jaw, as shown by F:AM 113264 (Figure 7) shows the typical morphology of most late Miocene peccaries. The lower incisors, i1 and i2, are small, peg-like, and pointed anterodorsally, and there are large canines which are even larger in males. The long curved post-canine diastema terminates in a cheek-tooth series with the classic bunodont pattern of nearly all Miocene tayassuines. The coronoid process is short and pointed strongly posterodorsally, with a short rounded articular process behind it. The angular region of the jaw has the robust ridge along the posteroverventral edge for the attachment of the strong temporalis and masseteric muscles.

When the type skull (F:AM 113317) and referred lower jaw (F:AM 113264) are articulated and viewed in anterior oblique orientation, the truly remarkable shape of the zygomatic flanges becomes even more apparent (Figure 7A).

A restoration of *Skimmerhyus shermerorum* is shown in Figure 8.

Discussion

As Wright (1993, 1998) pointed out, the late Clarendonian was a time of great diversification of peccaries, primarily due to the dramatic development of their zygomatic flanges and facial crests. Although the sample size is small in most taxa, we can be confident that these features are not solely due to sexual dimorphism, since there are several quarry samples where we have the zygomatic crests and flanges associated with both diagnostically male and female canines. According to Wright (1983), the sample of *Macrogenis crassigenis* shows this particularly well. In addition, we have the male skulls of *S. shermerorum* (F:AM 113316, 113317) versus the female skull (F:AM 113263). Thus, there appears to be regional diversification of tayassuid species in the late Clarendonian: *Woodburnehyus grenaderae* in California, *Skimmerhyus shermerorum* in the Plains, plus several species of *Macrogenis* in the Plains, and a new genus and species from Love Bone Bed in Florida that is still unnamed and undescribed (Wright, 1993, 1998).

The phylogenetic relationships of these peccaries and their nearest relatives are shown in Figure 9 (modified from Wright, 1993, 1998). As Wright noted, the *Macrogenis-Tayassu* clade is a monophyletic group of nearly all the higher peccaries. The next most derived clade on this cladogram is the node of the *Woodburnehyus-Skimmerhyus* clade, which is differentiated from more primitive *Macrogenis* by the distinctive facial crest of the zygoma extending anteriorly and dorsal to the P4. The *Woodburnehyus-Skimmerhyus* clade can be distinguished from all other peccaries by their distally angular, wing-like zygomatic flanges, whose anterior edges are straight and protrude perpendicularly from the faeial region of the snout (rather than sloping posteriorly back from the snout, as in nearly all other peccaries with flaring zygomatic arches, like *Macrogenis* and *Catagonus brachydontus*). Both *Woodburnehyus* and *Skimmerhyus* are distinct genera that cannot be referred to *Macrogenis* or any other existing taxon of peccaries due to the diagnostic combination of characters listed above, especially since their zygomatic flanges are so different in shape from each other and from all other known peccaries.

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